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A new genus of Late Cretaceous angel shark (Elasmobranchii; Squatinidae), with comments on squatinid phylogeny

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ABSTRACT

Three-dimensional Late Cretaceous elasmobranch endoskeletal elements (including palatoquadrates, ceratohyals, braincase fragments, and a series of anterior vertebrae) are described from the Late Cretaceous University of Alabama Harrell Station Paleontological Site (HSPS), Dallas County, Alabama. The material is referred to the extant elasmobranch Family Squatinidae on the basis of several distinctive morphological features. It also exhibits features not shared by any modern or fossil *Squatina* species or the extinct Late Jurassic squatinid *Pseudorhina*. A new genus and species is erected, despite there being some uncertainty regarding potential synonymy with existing nominal species previously founded on isolated fossil teeth (curiously, no squatinid teeth have been documented from the HSPS). A preliminary phylogenetic analysis suggests that the new genus falls on the squatinid stem, phylogenetically closer to *Squatina* than *Pseudorhina*. The craniovertebral articulation in the new genus exhibits features considered convergent with modern batomorphs (skates and rays), including absence of contact between the posterior basicranium and first vertebral centrum, and a notochordal canal which fails to reach the parachordal basicranium. Supporting evidence that similarities in the craniovertebral articulation of squatinoids and batomorphs are convergent rather than synapomorphic (as "hypnosqualeans") is presented by an undescribed Early Jurassic batomorph, in which an occipital hemicentrum articulates with the first vertebral centrum as in all modern sharklike (selachimorph) elasmobranchs. The fossil suggests instead that the bato-

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morph synarcual evolved by fusion of the anterior basiventral and basidorsal cartilages *prior* to the reduction of the anterior centra and loss of the occipital hemicentrum, not afterward as predicted by the hypnosqualean hypothesis.

INTRODUCTION

Modern squatinid elasmobranchs (angelsharks or monkfish; Order Squatiniformes Buen 1926, Family Squatinidae Bonaparte 1838) are highly specialized and morphologically distinctive (Carvalho et al., 2008; Claeson and Hilger, 2011), and there is both morphological and molecular support for modern squatinid monophyly (Douady et al., 2003; Stelbrink et al., 2010; Naylor et al., 2012). Some 20+ nominal extant squatinid species are recognized, all of which are currently classified in the genus *Squatina*.

The squatinid fossil record extends from the Late Jurassic and includes many isolated teeth (Cappetta, 2012), most of which are classified as *Squatina*. The distinctive gestalt (body form) of modern squatinids is easily recognizable in holomorphic fossils. Fragmentary but well-preserved three-dimensional fossils referred to the extant genus *Squatina* have been described from the Oligocene of Belgium (Mollen et al., 2016) and the Miocene of Japan and southern Argentina (Goto, 1977; Cabrera et al., 2012). Complete dorsoventrally flattened fossil skeletons of squatinids are known from the Late Jurassic of Germany, and incomplete skeletons are known from the Late Cretaceous of England (Woodward, 1888; Carvalho et al., 2008; Claeson and Hilger, 2011). Most holomorphic squatinid fossils have been referred either to the extant genus *Squatina* or to *Pseudorhina*, an extinct Late Jurassic taxon said to differ from *Squatina* in its basihyal morphology and tooth root structure (Carvalho et al., 2008). Some articulated Late Cretaceous fossils have been referred to a third genus (*Cretascyllium*) based on features of the dentition, although that taxon has also been considered a "subgenus" of *Squatina* (Guinot et al., 2012). Another Late Cretaceous genus (*Parasquatina*) has also been recognized, but is known only from teeth. From a phylogenetic perspective, *Pseudorhina* is recognizably a stem squatinid, but the systematic relationships of *Cretascyllium* and *Parasquatina* are less clear; they could fall either within the *Squatina* crown group or on the squatinid stem lineage (as could any number of extinct *Squatina* species founded on teeth).

The material described here is significant for several reasons. It represents the first Mesozoic squatinid from North America to be described from endoskeletal elements other than vertebrae; the material is, despite its incompleteness, arguably the best preserved of any Mesozoic squatinid described to date; the material is morphologically distinctive from all other described squatinids, suggesting that it represents a new taxon; and it represents the first squatinid fossil record from the University of Alabama Harrell Station Paleontological Site (HSPS), Marion Junction, Dallas County, Alabama (fig. 1).

The HSPS material was collected over many years and is cataloged as two lots under different numbers. According to ALMNH field notes, ALMNH 1040 was found in 1988 during Alabama Museum Expedition 10, while ALMNH 2792 was collected in 1992 on a staff field excursion in a different part of the HSPS property. Both lots consist of many

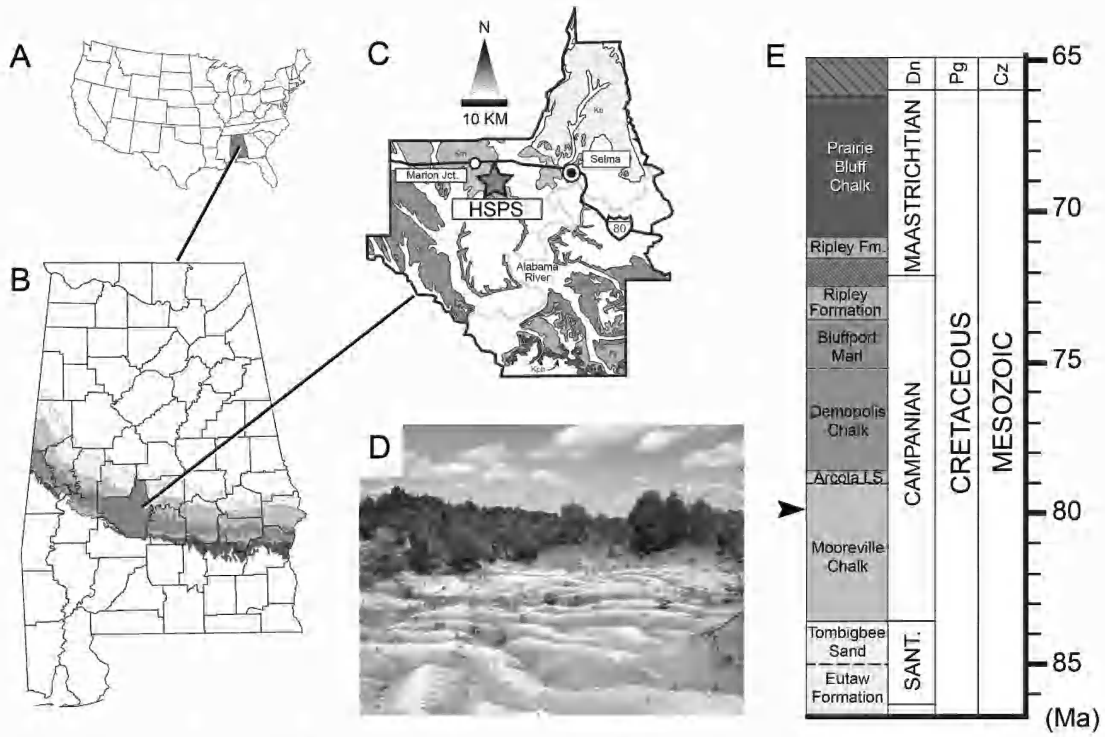

FIG. 1. Locality and stratigraphic information. **A,** location of Alabama within continental United States (no scale); **B,** location of Dallas County within Alabama (no scale); **C,** location (starred) of Harrell Station Paleontological Station (HSPS); **D,** general view of the HSPS site; **E,** Upper Cretaceous geologic section for western Alabama showing the approximate exposure level at HSPS (arrow).

small fragments of elasmobranch calcified cartilage, plus several larger, more complete skeletal elements. Much of the cartilage consists of unusually coarse tesserae (1–3 mm across), in contrast to most chondrichthyan TCC in which individual tesserae are often submicroscopic. In addition, rows of enlarged "voussoir" tesserae (sensu Maisey et al., in press) are present along margins of the first basiventral, and many of the larger tesserae have irregular zigzag borders rather than the usual subhexagonal close packing pattern.

Most of the Alabama material is disarticulated apart from a series of anterior vertebrae. Some fragments are freshly broken, but others show evidence of protracted surface erosion. The two lots (2792 and 1040) appear to represent parts of two different individuals, based on the size of corresponding elements and the lack of duplicate skeletal elements in each lot. For convenience of description, elements in each cataloged lot have been assigned suffixes (A, B, etc.).

The HSPS squatinid was originally referred to the sclerorhynchid *Ischyrhiza*, because distinctive teeth, rostral denticles, and a rostral cartilage of *I. mira* were already known from the same collecting area. However, none of the skeletal elements exhibits features characteristic of sclerorhynchids or other batoids (skates and rays); there is no vertebral fusion to form a batomorphlike synarcual cartilage (a synarcual is unknown in *Ischyrhiza*

but is present in other sclerorhynchids; e.g., *Libanopristis hiram*; Cappetta, 2012: fig. 367); palatoquadrate morphology is characteristic for squatinids and lacks features observed in modern and extinct batoids (which are classically characterized as "euhyostylic," with no direct connections between the palatoquadrate and cranium and the ceratohyal is decoupled from the hyomandibula; Gregory, 1904; Wilga, 2002). Additionally, no living or fossil batomorph is known with *Squatina*-like, tectospondylous vertebral centra.

The Harrell Station site is extensive, covering 142 acres of gullies cut into the Campanian Mooreville Chalk (unnamed member below the Arcola Limestone Member). Over many years of surface collecting, the site has produced numerous elasmobranch teeth, denticles, and vertebrae, plus chimaeroid tooth plates (*Edaphodon*, *Ischyodus*). No squatinid teeth have been found from the Harrell Station site, but teeth identified as *Squatina hassei* occur in the Tombigbee Sand (the unit below the Mooreville Chalk) approximately 10 miles north of HSPS, near Hamburg, Perry Co., Alabama.

An isolated squatinid anterior vertebra from either the Mount Laurel or Navesink Formation of Ramanessin Brook (Late Cretaceous; Campanian) in New Jersey is provisionally referred to the new taxon on the basis of features shared with the type specimen and considered autapomorphic for the new genus. Unfortunately, like many other fossils from the Ramanessin Brook locality, the vertebra was recovered from an outwash deposit rather than in situ and thus its precise stratigraphic horizon is uncertain. Squatinid teeth (usually identified as *Squatina hassei*) are also known from this locality.

RESULTS

Materials and Methods

Material Examined: ALMNH 1040, 2792, Late Cretaceous, Campanian, Mooreville Chalk, Harrell Station Paleontological Site, Marion Junction, Dallas County, Alabama. AMNH FF 22425, Late Cretaceous (Cenomanian-Maastrichtian), Mount Laurel or Navesink Formation, Ramanessin Brook, Holmdel, NJ: isolated first vertebra with bases of incomplete basiventral cartilages.

The first vertebral centrum of ALMNH 2792-C was subjected to computerized tomography using the GE Phoenix v|tome|x s240 scanner at AMNH. Scan parameters were as follows: voltage = 170 kV, current = 280 μA, filter 0.5 mm Cu, isotropic voxel size 0.05889734 mm. Data were reconstructed using datos|x reconstruction software (Phoenix|x-ray, release 2.0), then exported into a 16-bit TIFF image stack. Materialise Mimics Innovation Suite software version 18 was utilized for 3D reconstitution of the fossil.

Comparative views of modern squatinid endoskeletal elements were obtained from a specimen of *Squatina nebulosa*, AMNH 258172 (juvenile female 405 mm TL), scanned by J.S.S. Denton at the AMNH and segmented by C. Crawford. Comparison with *Cretascyllium cranei* was based on photographs of the holotype specimen (BNB 007329/007330), courtesy of C. J. Underwood.

An undescribed Early Jurassic batomorph examined by JGM in 2012 at the Stuttgart State Museum of Natural History in Germany (SMNS 52666) is also figured and discussed.

Institutional Abbreviations

ALMNH	Alabama Museum of Natural History, Tuscaloosa
AMNH	American Museum of Natural History, New York
BNB	Booth Museum, Brighton, U.K
SMNS	Stuttgart State Museum of Natural History, Germany

Anatomical Abbreviations

adf	adductor fossa of palatoquadrate
ant	anterior
artpr	articular process of palatoquadrate
bas	basicranium
bvpr	basiventral process (numbered sequentially)
c	centrum or centra (numbered sequentially)
cas	centrum anterior spool (vestigial)
ch	ceratohyal
con	occipital condyle (paired)
cot	cotylus (paired) on first basiventral to receive occipital condyle
cps	centrum posterior spool
dsulc	dental sulcus in palatoquadrate
f	foramen in fragmentary cranial cartilage
ihpr	interhyoideus process of ceratohyal
mb	main bar of palatoquadrate
Mc	Meckelian cartilage
medpr	median process of first vertebra
mpr	muscular process of palatoquadrate
nc	notochordal canal
och	occipital hemicentrum
orpr	orbital process of palatoquadrate
popr	postorbital process
post	posterior
pq	palatoquadrate
prcf	precerebral fossa of cranium
spc	spinal canal
sym	symphysis between paired jaw cartilages
syn	synarcual cartilage
vnr	ventral nerve root foramina in vertebrae

SYSTEMATICS

CLASS CHONDRICHTHYES HUXLEY, 1880

SUBCLASS ELASMOBRANCHII BONAPARTE, 1838

FAMILY SQUATINIDAE BONAPARTE, 1838

Cretasquatina new genus

This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:pub:168DD149-4390-4E54-9382-8084F7C39180.

DIAGNOSIS: Squatinid elasmobranch in which only the anteriormost two basiventrals of the vertebrae are expanded laterally. First basiventral process much broader distally than proximally, with rounded distal extremities and strongly recurved posterior borders surrounding the second basiventral and almost reaching the third centrum. Second basiventral process sharply angled posterolaterally, straight sided and slightly tapered distally. First vertebra with a vestigial anterior vertebral spool completely enclosed by the first basiventrals, notochordal canal does not reach anterior surface of first basiventral cartilage. Vertebral centra increase in width to centrum 5, then decrease in width. Palatoquadrate orbital process with smoothly rounded apex formed in tessellated cartilage and with a slight anterior projection on its anterolateral surface. Jaws smaller relative to the size of the occipital region than in other squatinids. Teeth unknown.

ETYMOLOGY: From the Latin *creta* ("chalk") plus *squatina* (Latin, "skate").

Cretasquatina americana, new species

DIAGNOSIS: As for genus.

ETYMOLOGY: From the Latinized version of the name *Amerigo*.

HOLOTYPE: ALMNH 2792 (figs. 2–4, 7, 10, 11), from the Early Campanian Mooreville Chalk (unnamed member below the Arcola Limestone Member), Harrell Station Paleontological Site, Marion Junction, Dallas County, Alabama: an associated series of six anterior vertebrae (ALMNH 2792-C; fig. 2), an almost complete left palatoquadrate approximately 125 mm long (ALMNH 2792-A), most of a ceratohyal approximately 120 mm long (ALMNH 2792-B), a small fragment of cartilage from the braincase, possibly part of the postorbital process (ALMNH 2792-D), plus numerous smaller indeterminate fragments of tessellated calcified cartilage (hereafter abbreviated to TCC).

REFERRED MATERIAL: ALMNH 1040 (fig. 8), including: almost complete right palatoquadrate approx. 143 mm long (ALMNH 1040-A); anterior part of left palatoquadrate (ALMNH 1040-B); two fragments of expanded arcualia from the first vertebra (ALMNH 1040-C); incomplete second vertebra (ALMNH 1040-D); vertebral centrum of uncertain position (ALMNH 1040-E.); heavily abraded vertebral centrum showing fine concentric rings (ALMNH 1040-F); numerous indeterminate fragments of calcified cartilage.

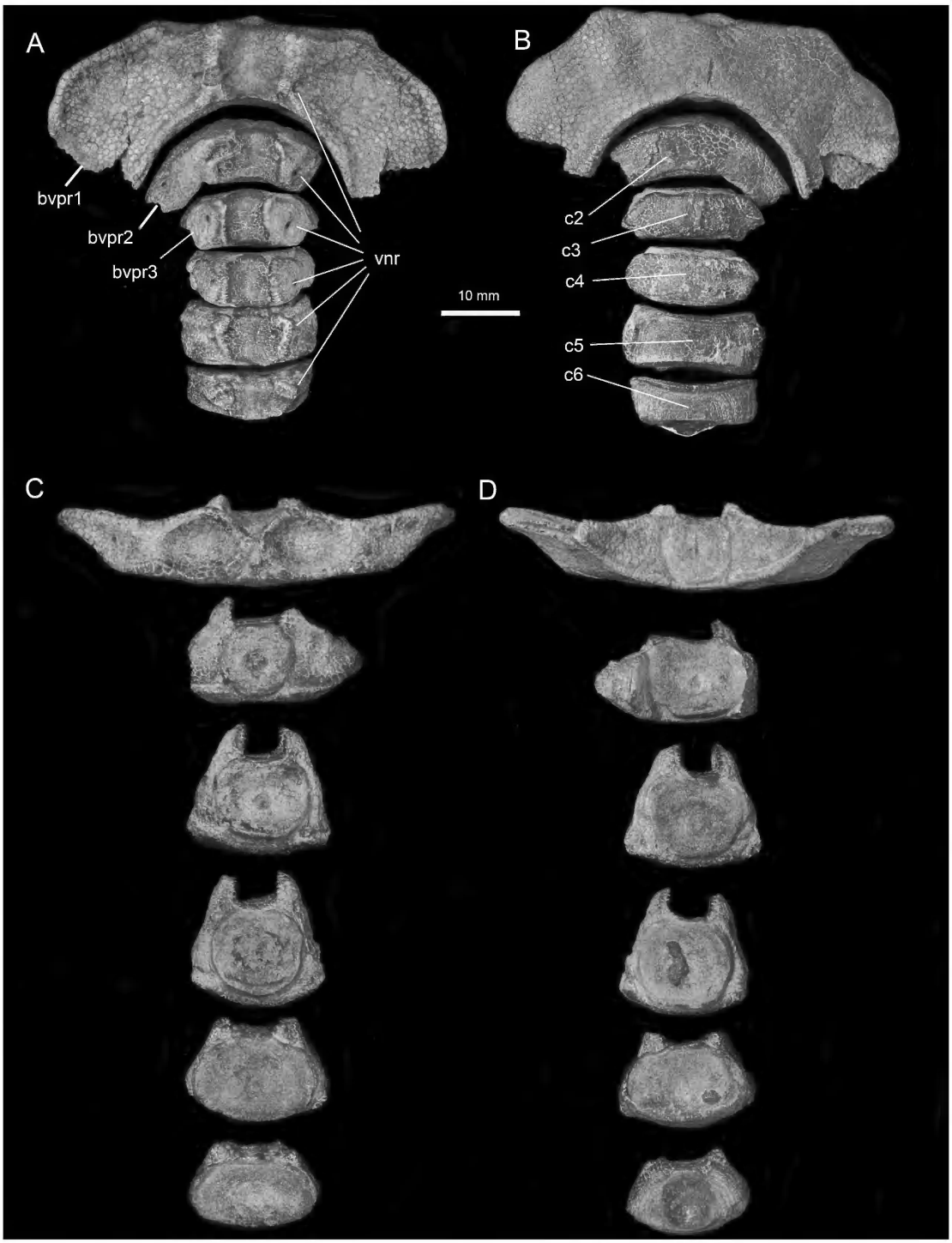

FIG. 2. *Cretasquatina americana*, gen. nov., sp. nov. Holotype, ALMNH 2792-C, six associated vertebrae forming the anterior vertebral complex: **A,** dorsal view; **B,** ventral view; **C,** anterior views of centra 1–6; **D,** posterior views of centra 1–6.

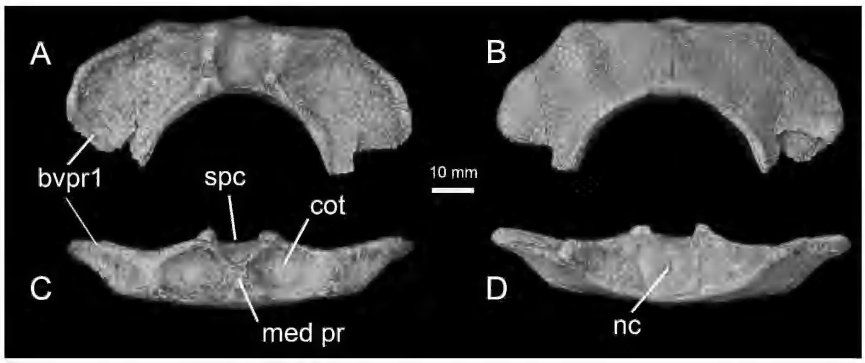

FIG. 3. *Cretasquatina americana*. Holotype, ALMNH 2792-C, first vertebra: **A,** dorsal view; **B,** ventral view; **C,** anterior view; **D,** posterior view. Note large size of individual tesserae.

Cretasquatina sp. indet.

Referred Material: AMNH FF 22425 (fig. 5); isolated and abraded first vertebra, Late Cretaceous, Cenomanian- Maastrichtian, Mount Laurel or Navesink Formation, Ramanessin Brook, Holmdel, NJ, collected by J. Kowinsky.

DESCRIPTION

Anterior Vertebrae: ALMNH 2792-C consists of an associated series of six heavily mineralized tectospondylous anterior vertebrae (fig. 2). The tectospondylous condition (with numerous fine concentric biomineralized layers) is considered a characteristic of squatinids; Ridewood, 1921; Shirai, 1992). The arcualia of adjacent vertebrae are unfused (i.e., a batoidlike synarcual is absent). The exposed posterior surface of the first centrum is slightly wider than tall, as are the anterior and posterior surfaces of the second centrum. The fifth and sixth centra have both suffered considerable erosion ventrally and thus appear oval as preserved, but were probably almost circular originally (the extent of erosion can be estimated from the position of the notochordal canal, which is normally central but now appears offset ventrally; fig. 2C, D).

The first vertebral centrum in ALMNH 2792-C is almost completely enclosed by TCC the basiventral and basidorsal cartilages, which merge laterally to leave only the posterior surface of the centrum exposed (figs. 2, 3). The anterior face of this element is entirely formed in TCC and bears a pyramid-shaped median process that is flanked by large paired oval cotyli (ALMNH 2792-C; figs. 3C, 4A). Each cotylus is slightly wider than tall and undoubtedly formed a broad articular surface for paired occipital condyles on the braincase, as in modern *Squatina* (fig. 5C, D; see also Vaz and Carvalho 2013: figs. 41D, 42D, 43D). The median process probably engaged with either a vestigial occipital hemicentrum or perhaps directly with a basioccipital fovea on the parachordal basicranium. There is no opening for the notochordal canal in its anterior face, but one is present posteriorly.

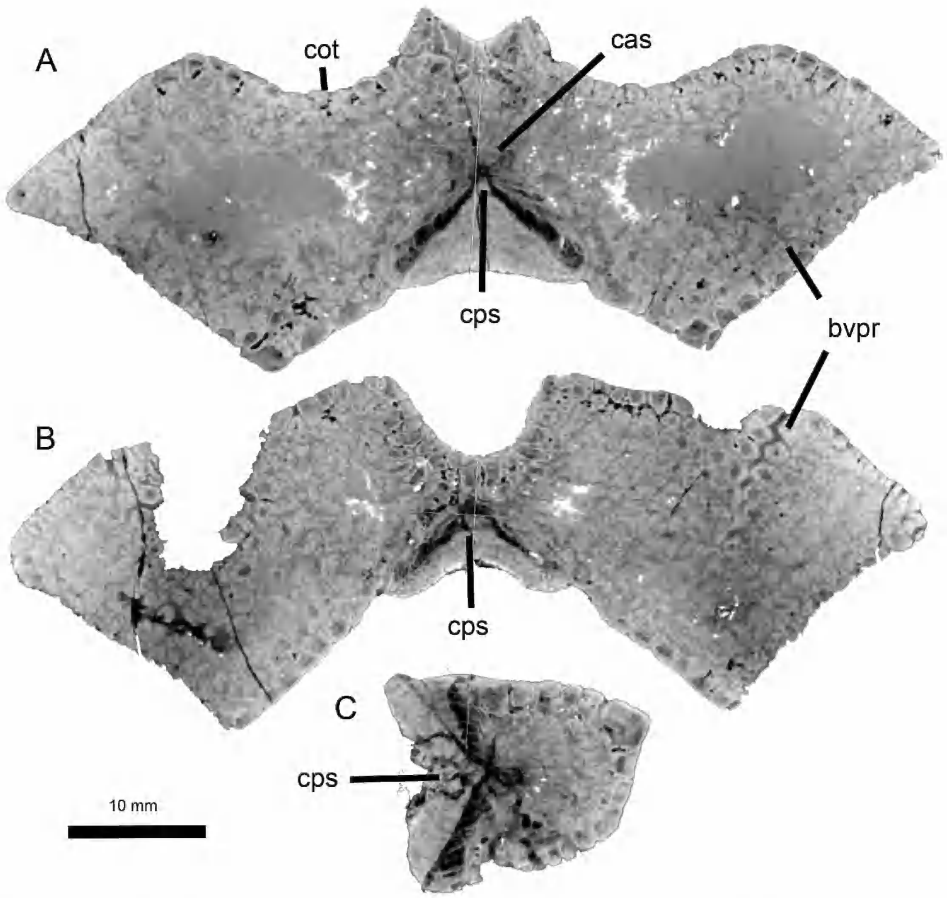

FIG. 4. *Cretasquatina americana*. Holotype, ALMNH 2792-C, computerized tomography images of slices through first vertebra: **A,** horizontal section through middle of centrum just above median process; **B,** slightly higher horizontal section clipping anterior part of spinal canal; **C,** midsagittal section through vertebral centrum. Note the extremely large size of individual tesserae, especially rows of "voussoir" tesserae along margins between adjacent surfaces.

Computerized tomography of the first vertebral centrum in ALMNH 2792-C reveals that the posterior spool is unreduced in size, although only its posterior face is exposed (fig. 4). By contrast, the anterior spool is greatly reduced and does not reach the anterior surface of the vertebra, and the notochordal canal passing axially through the centrum terminates anteriorly near the junction of the anterior and posterior spools, indicating that the notochord did not extend all the way to the occiput or enter the basicranium.

In modern squatinids, laterally expanded basiventrals are associated with the anteriormost three or four vertebrae and each expanded basiventral is as wide as or wider than the length of the associated centrum (Ridewood 1921; Claeson and Hilger, 2011: fig. 2; Vaz and Carvalho, 2013: fig. 47). The anterior basiventrals are also expanded in *Cretasquatina* and *Pseudorhina*, but their condition is unknown in *Cretascyllium*. In ALMNH 2792-C, laterally expanded basiventrals are present on vertebrae 1 and 2, but the processes of vertebrae 3–5 have been eroded,

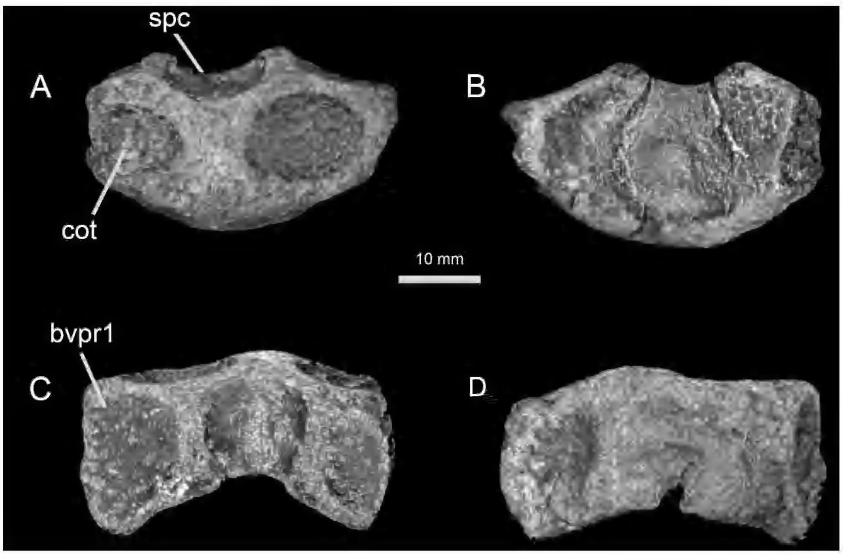

FIG. 5. AMNH FF 22425, Late Cretaceous, Ramanessin Brook, NJ; isolated first vertebra referred to *Cretasquatina*: **A,** anterior view; **B,** posterior view; **C,** dorsal view; **D,** ventral view. The centrum is visible posteriorly but does not emerge onto the anterior surface of the element. Large paired concavities of the cranial-vertebral articulation are present anteriorly. Note also the large size of cartilage tesserae covering surfaces of the arcualia and cotyli (compare with figs. 3, 4).

with only small remnants of calcified cartilage preserved. Nevertheless, based on the space available for these processes when the vertebrae are articulated (fig. 2A), only the first two basiventrals were probably expanded.

The anterior and posterior margins of the first basiventral process are strongly recurved posterolaterally and the lateral "wing" of the basiventral is expanded distally as far as the level of the third centrum, wrapping almost completely around the second basiventral laterally (figs. 2–4). By contrast, the first basiventral process in *Squatina* and *Pseudorhina* is only slightly deeper distally than proximally, with an almost straight rather than curved posterior margin; consequently the first basiventral does not wrap around the second centrum, the second basiventral is located almost completely behind the first, and more than two anterior basiventrals are expanded (usually three or four; fig. 5A, B and Claeson and Hilger, 2011: figs. 2B, D-F, 4; Vaz and Carvalho, 2013: fig. 47C).

Bases of the neural arches are preserved on vertebrae 1–6. Foramina for ventral nerve roots can be recognized on vertebrae 1–4 (fig. 2A). TCC extends from the bases of the neural arches, forming a floor to the main vertebral canal and separating it from the body of each centrum.

An incomplete vertebra from the Late Cretaceous of New Jersey, with a tectospondylous centrum typical of squatinids (AMNH FF 22425; fig. 5), shares two distinctive morphological features with ALMNH 2792-C. First, the vertebral centrum is exposed only on the posterior surface of the element and does not reach its anterior surface. By contrast, in *Squatina* and modern selachimorph elasmobranchs generally, the centrum extends to the anterior vertebral surface. Second, the basiventrals of this specimen are expanded anteroposteriorly and

have large paired cotyli anteriorly, as in the holotype of *C. americana*, Based on these similarities, this specimen is provisionally referred to *Cretasquatina* sp. indet.

In modern *Squatina*, the anterior spool of the first centrum is slightly narrower than the posterior one, but it still reaches the anterior face of the vertebra (Claeson and Hilger, 2011); in *Squatina* there is no median process, and the paired cotyli tend to be wider relative to their height than in *Cretasquatina* (fig. 6C). The anterior spool of the first centrum is unreduced in *Pseudorhina* (Claeson and Hilger, 2011: fig. 4D). This is the general condition among many living selachimorphs and probably represents a plesiomorphic state for squatinids (see Discussion).

PALATOQUADRATES: Specimen ALMNH 2792-A is a palatoquadrate from the left side, 125 mm long and 45 mm deep at the orbital process (fig. 7). It is well preserved in three dimensions, undoubtedly because the outer "rind" of TCC is extremely thick and individual tesserae are unusually large (between 2–8 mm across), making it a very robust element. ALMNH 1040-A (right palatoquadrate) represents a slightly larger individual than 2792-A (fig. 8A, B). ALMNH 1040-B (incomplete left palatoquadrate) includes only the anterior part of the tooth-bearing region (fig. 8C) that closely matches ALMNH 1040-A in size.

The palatoquadrate main bar (sensu Haller, 1926) has a slightly angular anterior end that is "finished" (i.e., it is completely surfaced by tesserae). Tesserae in chondrichthyans are generally absent where cartilages make direct contact or articulate with each other, so their presence on this surface suggests that there was no direct symphyseal contact between the palatoquadrates, although a stout symphyseal ligament may have been present, as in modern *Squatina*.

The buccal surface of the main bar includes a shallow dental sulcus, the floor of which is lined with TCC that exhibits hexagonal geometric close packing of individual tesserae. The dental sulcus in ALMNH 2792-A and 1040-A has seven shallow scalloped indentations, each separated by a low transverse ridge (figs. 7B, 8B). These indentations probably mark the approximate original position of tooth families, although this cannot be confirmed until specimens are found with teeth intact. Such indentations are generally absent in modern *Squatina* and seem to be absent in *Cretascyllium* and *Pseudorhina*. A "scalloped" dental sulcus is rarely found in modern elasmobranchs, but can be well developed in some Paleozoic chondrichthyans (e.g., *Cladodoides wildungensis*; Gross, 1937, 1938; *Cladodus elegans*; Ginter and Maisey, 2007).

In extant *Squatina*, each palatoquadrate typically supports 9–10 tooth rows, although *S. argentina* has 12 (Vaz and Carvalho, 2013). Only seven indentations for tooth families are present in the most complete palatoquadrates from HSPS (figs. 7A, 8A). Thus, it is possible that three or more tooth families were crowded into the anteriormost indentation. The parasymphseal and next two adjacent tooth families in modern *Squatina* are sometimes crowded into a space that is only as wide as the fourth tooth family (e.g., *S. nebulosa*; fig. 9D, E). In many living and extinct squatinids, the tooth-bearing part of the palatoquadrate usually extends posteriorly to the level of the orbital process. However, in *Cretascyllium*, no teeth seem to be present behind the level of the orbital process and its dental sulcus apparently ends below rather than posterior to the process (Guinot et al., 2012: fig. 2).

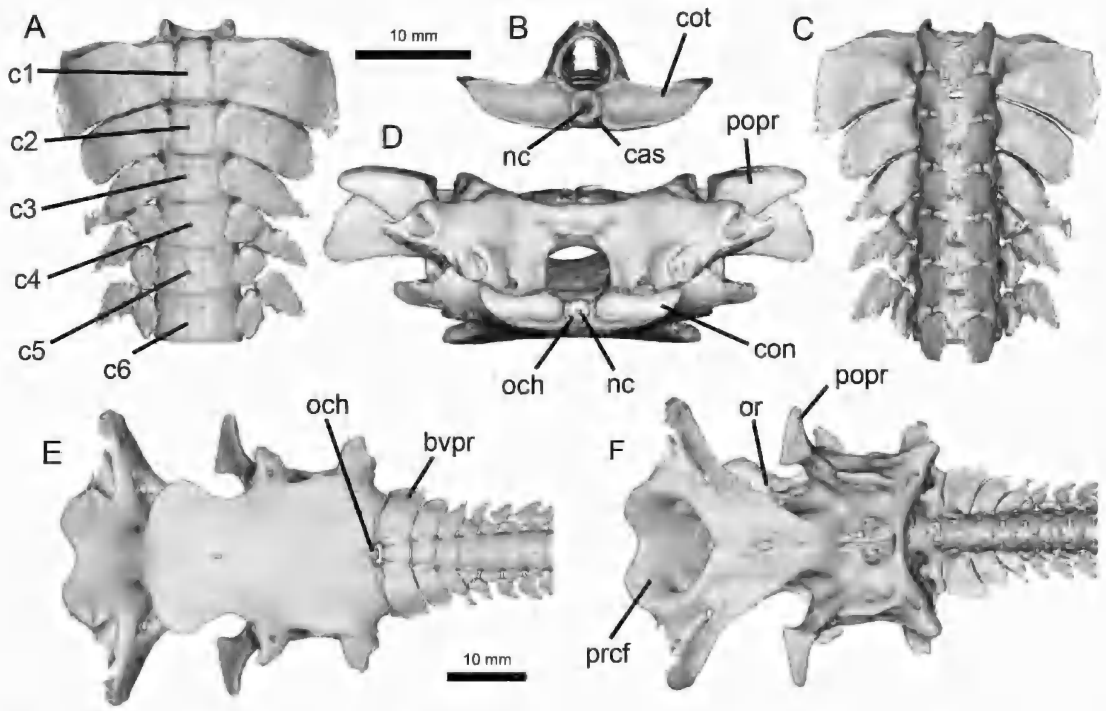

FIG. 6. *Squatina nebulosa*, AMNH 258172. Views of the cranium and anterior part of vertebral column, imaged from tomographic scan by C. Crawford: **A,** ventral view of first six vertebral centra and associated basiventrals, anterior to top; **B,** anterior view of first vertebral element; **C,** dorsal view of A; **D,** posterior view of cranium; **E,** ventral view of cranium and vertebral centra (anterior to left); **F,** dorsal view of same. Upper scale bar for A–D; lower scale bar for E and F only.

In ALMNH 2792-A and 1040-A, there is a stout and broad-based orbital process, with slightly concave anterior and posterior margins, and a domelike apex covered by subhexagonal tesserae (again indicating that this part of the cartilage was "finished"). The rounded apex of the process has a smooth, slightly polished outer surface, contrasting with the dull, matte surface of tesserae on more proximal parts of the process. The anterolateral part of the apex extends slightly beyond the anterior border of the process, giving rise to a ridge that diminishes in height posteriorly and does not continue onto on the mesial surface of the process (figs. 7A, 8A).

The palatoquadrate orbital process in modern *Squatina* is slender and forms a sliding articulation with the outer wall of the orbit (fig. 9C). A corresponding articulation in *Squalus* not only maintains a connection between the upper jaw and cranium, but also acts to restrict palatoquadrate motion during jaw protraction (Wolfram, 1984). The orbital process in *Squatina* has sometimes been characterized as extending dorsally through a recess or fenestra in the supraorbital cartilage, an arrangement generally considered apomorphic for squatinids (Shirai, 1992; Carvalho et al., 2008). However, the distal part of the "process" in *Squatina* is not cartilaginous, but instead consists of ligamentous tissue external to the perichondrium. The cartilaginous component of the orbital process is actually quite short in modern *Squatina*, and thus may not really extend as far as the supraorbital cartilage (fig. 9A, C).

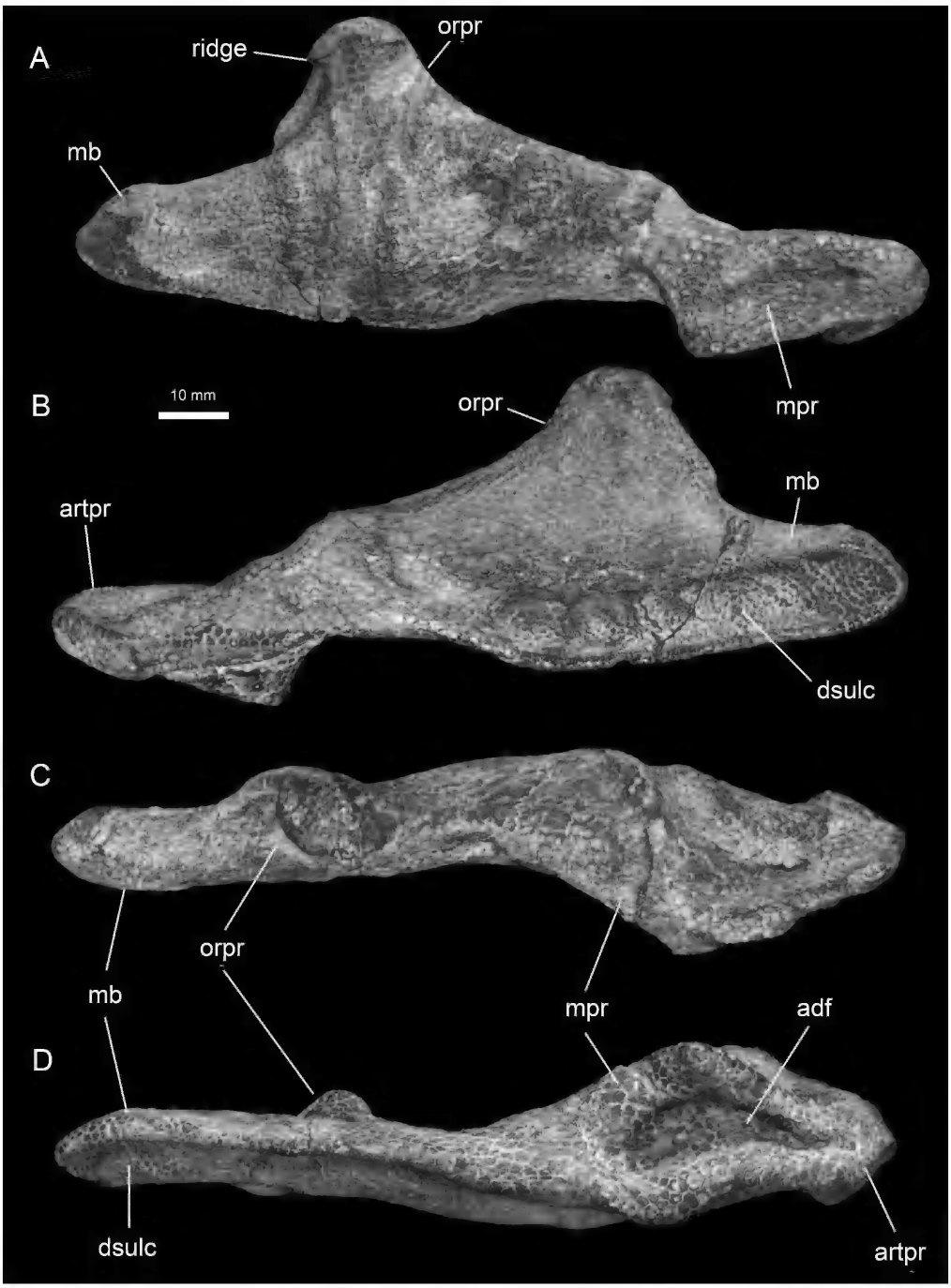

FIG. 7. ALMNH 2792-A, almost complete left palatoquadrate, referred here to *Cretasquatina americana*: **A,** lateral view, anterior to left; **B,** mesial view, anterior to right; **C,** dorsal view, anterior to left; **D,** ventral view, anterior to left. Note extremely large cartilage tesserae (some with zigzag intertesseral contacts), especially in the center of the lateral surface of the palatoquadrate main bar in A.

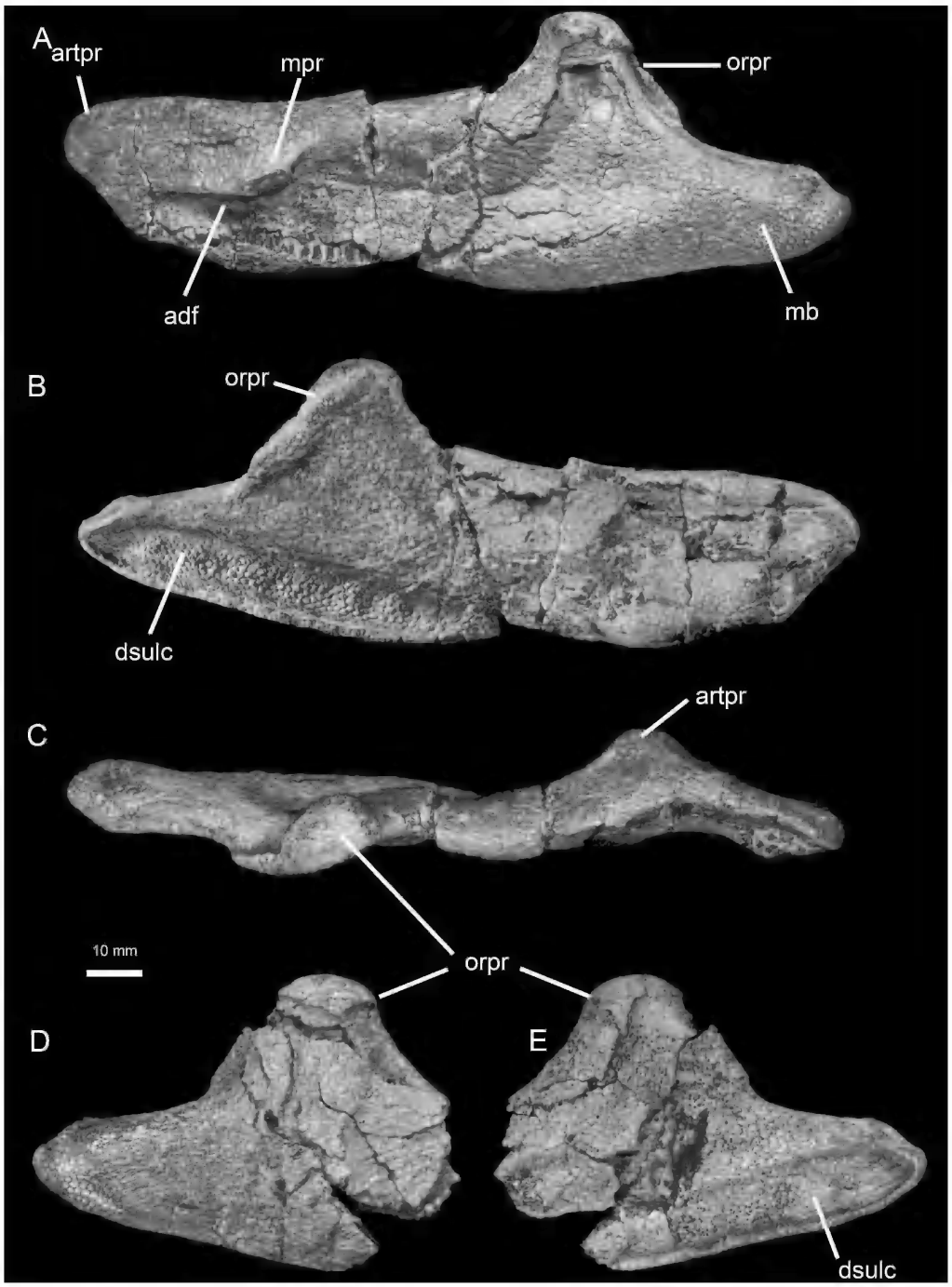

FIG. 8. Additional palatoquadrates referred here to *Cretasquatina americana*: A–C, ALMNH 1040-A, almost complete right palatoquadrate approximately 143 mm long. **A,** lateral view, anterior to right; **B,** mesial view, anterior to left; **C,** dorsal view, anterior to left; **D, E,** ALMNH 1040-B, anterior part of left palatoquadrate matching 1040-A in size and representing its antimere (the two were collected together).

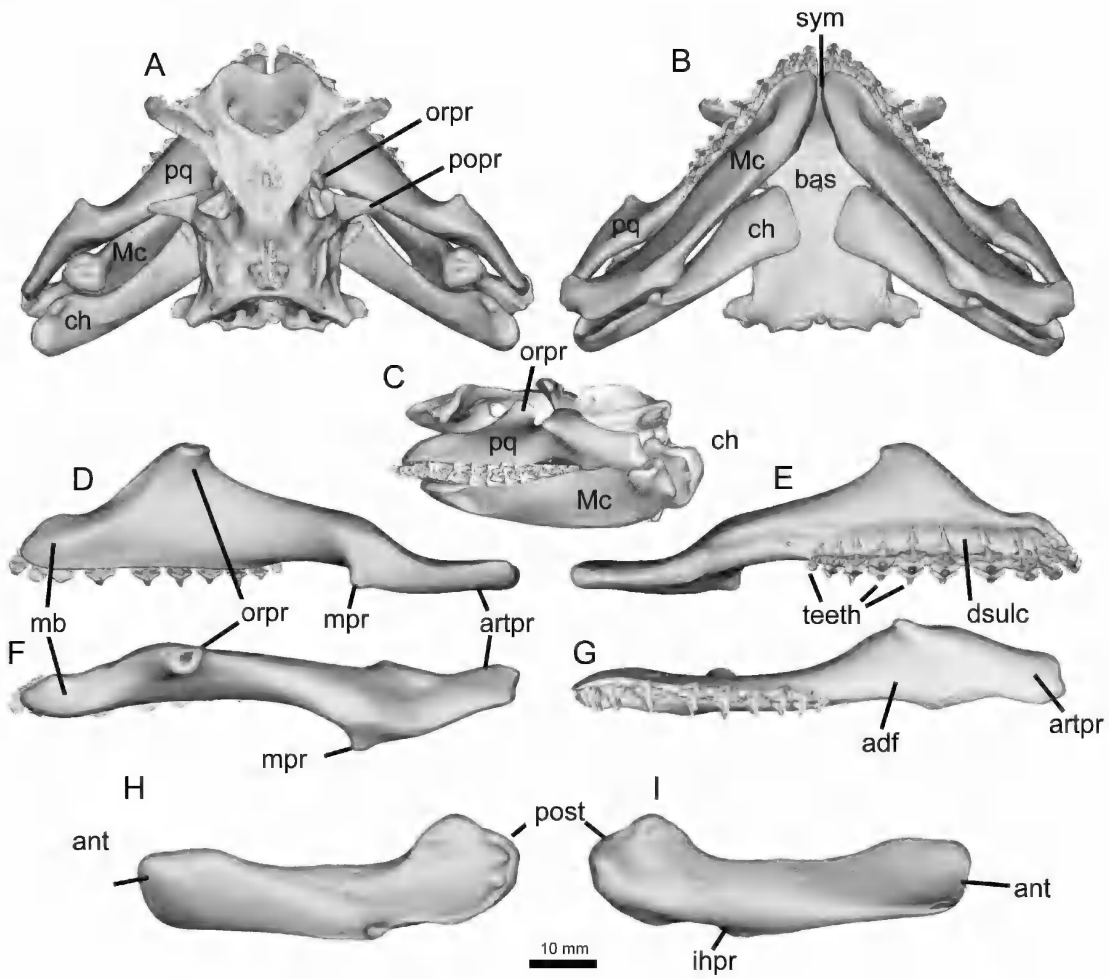

FIG. 9. Head skeleton of modern *Squatina nebulosa*, AMNH 258172 (juvenile female 405 mm TL), images from scanned specimen segmented by C. Crawford: **A,** cranium, jaws and ceratohyals in dorsal view, anterior to top; **B,** same in ventral view; **C,** same in lateral view, left side, anterior to left; **D,** left palatoquadrate in lateral view, anterior to left; **E,** same in mesial view, anterior to right; **F,** same in dorsal view, anterior to left; **G,** same in ventral view, anterior to left; **H,** left ceratohyal in lateral view; **I,** same in mesial view.

In fossil squatinids, the noncartilaginous distal part of the orbital process is usually not preserved. The preserved height of the cartilaginous process is thus an unreliable indicator of the full original extent of the structure (including its ligamentous portion). In *Pseudorhina acanthoderma,* the low, rounded cartilaginous orbital process is confined to the anterior part of the orbit, but there is a distinct notch or recess for the orbital articulation at the base of the postorbital process farther posteriorly (Carvalho et al., 2008: fig. 6A). This observation suggests that there was an extensive ligamentous extension to the orbital process that is not preserved in the fossils.

The rounded apex the cartilaginous palatoquadrate orbital process in ALMNH 2792-A and 1040-A is directed dorsally and has a slight lip where it overhangs the orbital process

FIG. 10. ALMNH 2792-B, three views of ceratohyal referred here to *Cretasquatina americana*. Anterior to right in A and C, to left in B. Again, note the extremely coarse texture of tesserae.

anterolaterally (figs. 7A, 8A). The process is also dorsally directed in *Pseudorhina acanthoderma* (Carvalho et al., 2008: fig. 6), but it does not protrude anteriorly. In modern *Squatina*, the calcified part of the process is directed posterodorsally rather than dorsally, and lacks an anterior protrusion like that found in ALMNH 2792-A and 1040-A (figs. 6A, 7A, 8D, E). The cartilaginous orbital process projects posterodorsally in *Cretascyllium cranei* (Guinot et al., 2012: fig. 2), but the shape of its apex is unknown.

The muscular process (sensu Haller, 1926; = "Muskelforsatz" of Gegenbaur, 1872; "postorbital process" of Shirai, 1992; "quadrate process" of Carvalho et al., 2008) in modern squatinids is short, with a low, rounded apex directed anterolaterally (fig. 8). The adductor fossa in modern *Squatina* is comparatively shallow, although it is still roofed in part by the muscular process (fig. 9D–G). Having the adductor fossa partly roofed by the muscular process is an unusual arrangement in modern elasmobranchs and may be an autapomorphy of squatinids (Shirai, 1992: char. 30). The muscular process in ALMNH 2792-A and 1040-A overhangs a deep adductor fossa (figs. 7D, 8A). The fossa is elongated

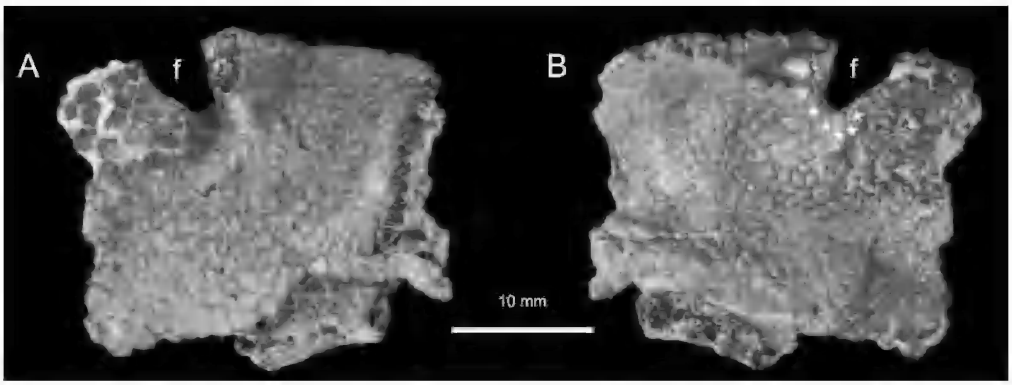

FIG. 11. ALMNH 2792-D, fragment of braincase, possibly part of the postorbital process. Small white stars in B mark a series of voussoir tesserae lining the outer margin of a foramen.

anteroposteriorly but is relative short vertically. The adductor fossa extends farther anteriorly in ALMNH 2792-A and 1040-A than in modern *Squatina*. However, the muscular process has been described as overhanging the adductor fossa dorsolaterally in various Mesozoic and Paleozoic hybodont sharks (Maisey, 1982, 1983). Hybodonts are considered to be extinct stem elasmobranchs and are not related to squatinids within the elasmobranch crown (Maisey et al., 2004), and the "overhanging" muscular process is therefore considered evolutionary convergence to squatinids, perhaps related to similarities in their adductor muscle action.

In both ALMNH 2792-A and 1040-A, the articular process (sensu Hotton, 1952) of the palatoquadrate lacks a quadrate concavity for the lower jaw, a feature shared with modern *Squatina* and some other modern sharks (e.g., *Squalus*). As noted by Haller (1926) and Wolfram (1984), this occurs when the quadrate concavity is formed entirely within fibrous connective tissue mesial to the palatoquadrate cartilage, not on the cartilage itself.

Palatoquadrate proportions in *Cretasquatina americana* (based on ALMNH 2792-A) were compared to those of modern *Squatina nebulosa* and the fossil squatinids *Pseudorhina acanthoderma* and *Cretascyllium cranei* (fig. 12). The images in this figure are not to scale and have been adjusted so that all the elements have equivalent length (except for *C. cranei*, in which the posterior articular process is missing and overall palatoquadrate length therefore had to be estimated). While their overall morphology is similar, differences were observed in the position of the orbital and muscular processes. In ALMNH 2792-A and *S. nebulosa*, the orbital process is located farther posteriorly relative to the symphysis than in *P. acanthoderma*. However, the muscular process in *S. nebulosa* and *P. acanthoderma* is situated farther anteriorly, relative to the articular process, than in ALMNH 2792-A. Since the muscular process defines the anterior extent of the adductor fossa, the attachment surface of this muscle was apparently shorter relative to overall palatoquadrate length than in *S. nebulosa* and *P. acanthoderma*. It was not possible to determine palatoquadrate proportions accurately in *C. cranei*, but the relative positions of its orbital and muscular processes resemble the arrangement in modern *Squatina* rather than in *Pseudorhina* (where

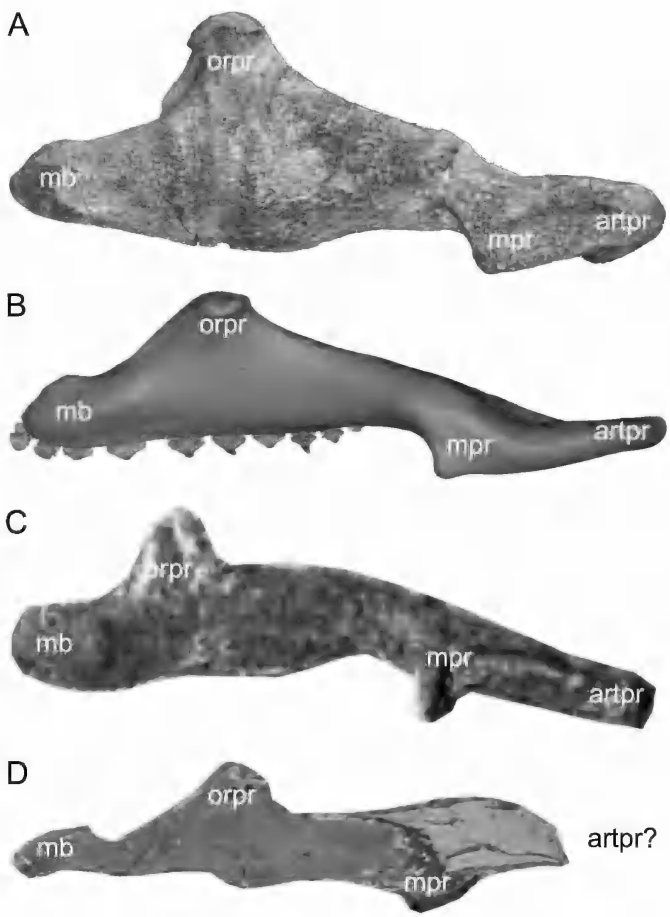

FIG. 12. Comparison of palatoquadrate proportions in four different squatinids, all in lateral view, anterior to left. See text for discussion. **A,** ALMNH 2792-A (see fig. 6), referred here to *Cretasquatina americana*; **B,** modern *Squatina nebulosa*, AMNH 258172 (see fig. 9); **C,** *Pseudorhina acanthoderma* (adapted after Vaz and Carvalho, 2013; fig.6); **D,** *Cretascyllium cranei* (adapted from a photograph of the holotype specimen, Booth Museum BNB 007329/007330, courtesy of C.J. Underwood).

the orbital process is located farther anteriorly) or ALMNH 2792-A (where the mandibular process is located farther posteriorly).

Ceratohyal: The element identified here as a ceratohyal (fig. 10: ALMNH 2792-B) has a pronounced curvature, with a length of c145 mm along its convex ventral margin. According to Vaz and Carvalho (2013), the ceratohyal in modern *Squatina* is only 2/3 the length of Meckel's cartilages, which are approximately as long as the palatoquadrates. However, ALMNH 2792-B is almost as long as the associated palatoquadrate (ALMNH 2792-A), possibly because the palatoquadrate articular process in *Cretasquatina* was apparently shorter than in modern *Squatina*. Ceratohyal ALMNH 2792-B is more slender relative to its length than in modern *Squatina* (figs. 8, 9; also cf. *S. californica*, *S. occulta*, *S. guggenheim*; Carvalho et al., 2008: fig. 4C, D; Vaz and Carvalho, 2013: figs. 45, 46). According to Carvalho et al. (2008), the ceratohy-

als of *Pseudorhina* are also more slender than in modern *Squatina*. Ceratohyal proportions are unknown in other extinct squatinids, but a comparatively robust ceratohyal may be an apomorphic feature that unites *Squatina* and some other extinct squatinids.

Both ends of the ceratohyal ALMNH 2792-B are intact, but part of its ventral margin is broken. In modern *Squatina*, the ceratohyal ventral margin bears a prominent process for the insertion of the interhyoideus muscle (fig. 9I; see also Vaz and Carvalho, 2013), but this cannot be observed in the fossil. The distal end of the ceratohyal has a wide flattened surface, presumably forming an articular surface with the basihyal. The proximal end of the ceratohyal is almost complete and has an articular surface for the hyomandibula. Unfortunately, the hyomandibula and basihyal elements are not preserved.

Braincase Fragment: A single fragment of cartilage, approx. 25 × 28 mm in size, is identified as part of the braincase wall based on its arched cross section and the presence of a large but incomplete foramen (fig. 11). Cartilage surrounding one side of this foramen is raised, forming a broken process. It is uncertain which part of the braincase is represented, but it could be part of the postorbital wall adjacent to the hyomandibular branch of the facial nerve. The concave surface is interpreted as the intracranial wall. It is lined by subhexagonal tesserae ~1–1.5 mm across, with a row of voussoir tesserae forming the inner margin of the foramen. Tesserae on the convex (presumably external) surface of the cartilage have irregular margins and gradually increase in size toward the foramen, without a voussoir series.

Cartilage Mineralization: The fossils exhibit the characteristic tessellated biomineralized tissue found in modern elasmobranch cartilage, in which innumerable tilelike blocks (tesserae) are held together in life by a geodesic framework of collagenous fibers (Seidel et al., 2016). However, modern elasmobranch tesserae are often microscopic (often less than 1.0 mm across; Debiais-Thibaud, 2019), i.e., much smaller than in *Cretasquatina*, where they are routinely 2–3 mm or more in diameter. Tesserae forming the visceral arch elements in *Cretasquatina* also exhibit interlocking zigzag contacts, and some tessellated surfaces appear "stretched" unidirectionally (figs. 6A, 7A, 9). It is unclear what mechanical or other biological advantages were gained from having such large tesserae, but this unusual property may have contributed to their preservation, by providing greater resistance to postmortem collapse, taphonomic disintegration, and erosion.

Similar large tesserae have not been reported previously in other squatinid fossils, but are nevertheless evident in published illustrations (e.g., Guinot et al., 2012; Mollen et al., 2016). By contrast, tesserae in *Pseudorhina alifera* seem to be small, as in elasmobranchs generally (Carvalho et al., 2008, fig. 15A). Tesseral size has not been investigated in modern *Squatina*.

Rows of voussoir tesserae are present in *Cretasquatina* along the margins of the first basiventrals, the outer oral margin of the palatoquadrates, and apparently around cranial foramina. Enlarged and voussoir tesserae are uncommon in modern elasmobranchs, although their systematic distribution has never been surveyed. It is unknown whether they serve a functional role, and/or if they exhibit any systematic pattern of distribution.

PHYLOGENETIC ANALYSIS

Phylogenetic analysis to infer the placement of *Cretasquatina* was conducted on a matrix of eight taxa and 19 unordered morphological characters, 15 of which were parsimony informative. Taxa included in the analysis were *Squalus*, *Pristiophorus*, *Raja*, an undescribed Lower Jurassic batoid (SMNS 52666), *Pseudorhina*, *Cretasquatina*, *Cretascyllium*, and *Squatina*. Except as indicated below, characters were drawn from previous literature (Maisey, 1980; Shirai, 1992, 1996: Carvalho, 1996; Carvalho et al., 2008; Claeson, 2010).

1. Orbital articulation: (0) absent (1) present.

2. Pectoral propterygium orientation: (0) extending posterolaterally (1) extending anteriorly.

3. Pectoral propterygium extent: (0) not reaching olfactory capsule (1) reaching capsule.

4. Nasal capsule: (0) directed anteriorly (1) expanded laterally.

5. Lower labial cartilage: (0) small (1) broad.

6. Quadrate process of palatoquadrate: (0) vertical (1) directed laterally.

7. Anteroposterior length of first basiventral: (0) equal to or only slightly longer than second BV (1) two to three times longer than second BV.

8. Anterior lobe cartilage of pectoral fin: (0) absent (1) present.

9. Postorbital process: (0) directed laterally (1) directed anteriorly.

10. Palatoquadrate orbital process (absent in *Scyliorhinus*, *Raja*; unknown in SMNH 52666): (0) nearly vertical (1) obliquely inclined anteroposteriorly.

11. Tip of orbital process (inapplicable for *Scyliorhinus*, *Raja*; unknown in SMNH 52666): (0) facing dorsally (1) facing posterodorsally.

12. Tectospondylous vertebral centra (sensu Ridewood, 1921): (0) absent (1) present.

13. Notochordal canal reaches occipital region: (0) present (1) absent.

14. Anterior spool of first vertebral centrum (inapplicable for *Raja*): (0) unreduced (1) smaller than posterior spool (new character).

15. Anterior spool of first centrum (inapplicable for *Raja*): (0) contributes to craniovertebral articulation (1) does not reach occiput or contribute to articulation (new character).

16. Basiventrals 1 and 2 wider than diameter of corresponding centrum (inapplicable for batoids): (0) absent (1) present (new character).

17. Basiventral 3 wider than diameter of corresponding centrum (inapplicable for *Raja*): (0) absent (1) present (new character).

18 First basiventral (inapplicable for *Raja*): (0) entirely anterior to second (1) recurves around second basiventral (new character).

19. Synarcual: (0) absent (1) present.

The taxa *Cretascyllium* (42% missing), *Cretasquatina* (37% missing), and SMNH 52666 (21% missing) accounted for the entirety of the missing data in the matrix.

Taxa and characters were coded as follows:

										1	1	1	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Squalus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raja	0	1	1	0	0	0	-	0	0	-	-	0	1	-	-	-	-	-	1
SMNS 52666	0	1	0	?	?	?	0	?	0	-	-	0	0	0	0	0	0	0	1
Pristiophorus	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Pseudorhina	1	1	0	1	1	1	0	1	0	1	0	1	0	0	0	1	0	0	0
Cretasquatina	1	?	?	?	?	1	1	?	?	1	0	1	1	1	1	1	?	1	0
Cretascyllium	1	1	0	?	?	1	?	?	1	1	1	1	0	?	0	?	?	?	0
Squatina	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0

Analysis was conducted using a heuristic search under the unweighted parsimony criterion in PAUP* (Swofford, 2002), with *Squalus* as the outgroup taxon. Starting trees were obtained by stepwise addition, with 100 trees held at each step. Search was conducted using TBR branch swapping, swapping on all trees, with a reconnection limit of 20. Following heuristic search, 1000 bootstrap replicates were conducted.

The analysis produced two topologies of length 22 (consistency index [CI] = 0.863; retention index [RI] = 0.842; rescaled consistency index [RCI] = 0.727). A strict consensus topology, along with bootstrap support values, is presented in figure 13. A monophyletic squatinid total group was recovered, in which three extinct taxa (*Pseudorhina*, *Cretasquatina* and *Cretascyllium*) are successive sister taxa to extant *Squatina*. *Pseudorhina* is recovered as the earliest-diverging member of the group, corroborating previous findings (Carvalho et al., 2008; Claeson and Hilger, 2011; Vaz and Carvalho, 2013; Mollen et al., 2016). The relationships of pristiophorids, squatinids, and batomorphs were unresolved.

DISCUSSION

Our phylogenetic analysis (using an admittedly limited morphological data set) retrieved a monophyletic grouping that includes the squatinid crown group (represented by *Squatina*) and a squatinid stem that is populated successively by *Pseudorhina* (the most basal taxon), *Cretasquatina*, gen. nov., and *Cretascyllium*. Our placement of *Cretascyllium* outside the squatinid crown group challenges the view of Guinot et al. (2012) that it represents a subgenus of *Squatina* within the squatinid crown. The squatinid total group (i.e., stem plus crown) is characterized in this analysis by at least three unambiguous synapomorphies (chars. 6, 10, 12; laterally directed quadrate process, obliquely inclined orbital process, tectospondylous vertebrae). Three other potential synapomorphies of the squatinid total group (chars. 4, 5, 8; laterally expanded nasal capsule, broad lower labial cartilage, pectoral anterior lobe cartilage present) are presently unknown in *Cretasquatina* and *Cretascyllium*.

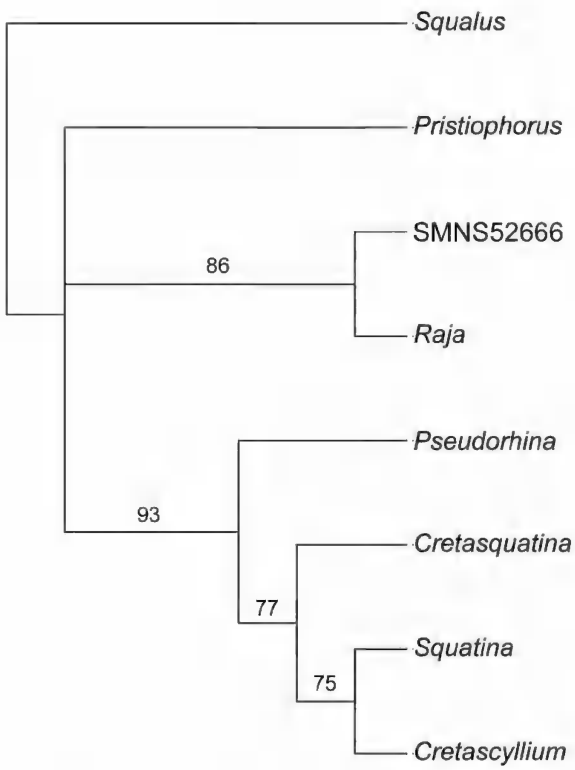

FIG. 13. Strict consensus of two equally parsimonious trees, inferred from PAUP*. Numbers at nodes are bootstrap support values. *Cretasquatina* is inferred to lie on the squatinid stem above *Pseudorhina*. *Cretascyllium* is resolved in this analysis as the closest extinct taxon to modern *Squatina*.

Although *Cretasquatina* is undoubtedly a squatinid, it differs from all other squatinids as follows; the anterior spool of the first free vertebral centrum is vestigial (although the reduced size of the anterior spool in *Squatina* and *Cretasquatina* is a potential synapomorphy not shared with *Cretascyllium* or *Pseudorhina*); the notochordal canal terminates behind the occiput; the basiventral processes extend behind the second centrum; only the first two basiventrals are expanded; the palatoquadrate dental sulcus exhibits several scalloped indentations; and the orbital process of the palatoquadrate has a smoothly rounded apex with a weak anterior projection on its anterolateral surface. In addition, the paired cotyli forming the lateral parts of the craniovertebral articulation on the anterior face of the first vertebra in *Cretasquatina* are narrower than in modern *Squatina*, but this feature is unknown in other extinct squatinids.

In all modern selachimorph elasmobranchs apart from the sawsharks (Pristiophoridae), the neurocranial component of the craniovertebral articulation is formed by an occipital hemicentrum (representing the posterior spool of a "typical" elasmobranch vertebral centrum), which is located within a concave space (basioccipital fovea; Shirai, 1992, 1996; Carvalho, 1996; Maisey et al., 2004; Claeson and Hilger, 2011). The systematic distribution of the hemicen-

trum and fovea are two crucial characters at the core of the "hypnosqualean" hypothesis (first advanced by Shirai, 1992), according to which absence of the basioccipital fovea unites modern squatinids, pristiophorids, and batomorphs (his char. 52), and the absence of an occipital hemicentrum further unites pristiophoroids and batomorphs (his char. 53).

Claeson and Hilger (2011) have shown that the basioccipital fovea and occipital hemicentrum are both present in modern *Squatina*, and that the occipital hemicentrum in the Late Jurassic *Pseudorhina* is unreduced. They also speculated that a prominent notch in the posterior basicranium ventral to the foramen magnum in modern and extinct batomorphs (= "median articular facet"; El-Toubi and Hamdy, 1959) may be homologous with the basioccipital fovea in selachimorphs, and suggested that absence of the fovea could be autapomorphic for Pristiophoriformes among modern elasmobranchs, rather than a synapomorphy shared with batomorphs. The median articular facet in batomorphs engages with a ventral anterior process of the synarcual and is flanked by paired occipital condyles, and thus corresponds topographically with the basioccipital fovea of modern selachimorphs in which an occipital hemicentrum is present, and with the fovea in extinct chondrichthyans where biomineralized centra are absent (e.g., *Hybodus*, *Orthacanthus*, *Tamiobatis*). Like the basioccipital fovea in selachimorphs, the median articular facet of modern batomorphs forms embryonically in the posterior margin of the parachordal cartilage and is recognizable even at early ontogenetic stages in embryonic batomorphs (e.g., *Raja*, 46 mm; *Torpedo*, 24 mm; *Urolophus*, 33 mm; Holmgren, 1940).

The morphology of the first vertebral centrum in *Cretasquatina* brings a new wrinkle to the "hypnosqualean" controversy, by revealing that the craniovertebral articulation in some early squatinids lacked direct connection via the first free centrum and occiput, and that the notochord failed to reach the basicranium (as in modern batoids, but unlike modern *Squatina* and pristiophorids). Unfortunately, it is still unknown whether *Cretasquatina* possessed or lacked an occipital hemicentrum, although one is present in living *Squatina* and in *Pseudorhina alifera* (Claeson and Hilger, 2011: figs. 2, 4). Furthermore, the notochordal canal in *Pseudorhina* apparently passes completely through the first vertebral centrum (Claeson and Hilger, 2011). From these collective observations, it is concluded that *Cretasquatina* is convergent with modern batomorphs in having no centrum-to-centrum connection at the craniovertebral articulation, and a notochordal canal that does not reach the cranium.

This postulated convergence is corroborated by an undescribed Early Jurassic fossil in the collection of the Stuttgart State Museum of Natural History (fig. 14), resolved in our phylogenetic analysis as a batomorph sister taxon to *Raja*. The synarcual cartilage in modern batomorphs is a compound structure, composed of fused basidorsal and basiventral arcualia enclosing a variable number of vertebral centra that are absent in the anteriormost axial segments. By contrast, a selachimorphlike occipital hemicentrum is present (presumably within a basioccipital fovea, although this requires confirmation) in SMNS 52666. Furthermore, the hemicentrum articulates with the first of four unreduced anterior vertebral centra that are enclosed by a short synarcual cartilage (which clearly comprises the anteriormost four paired basiventrals). In certain other extinct batomorphs, an occipital hemicentrum is absent, but

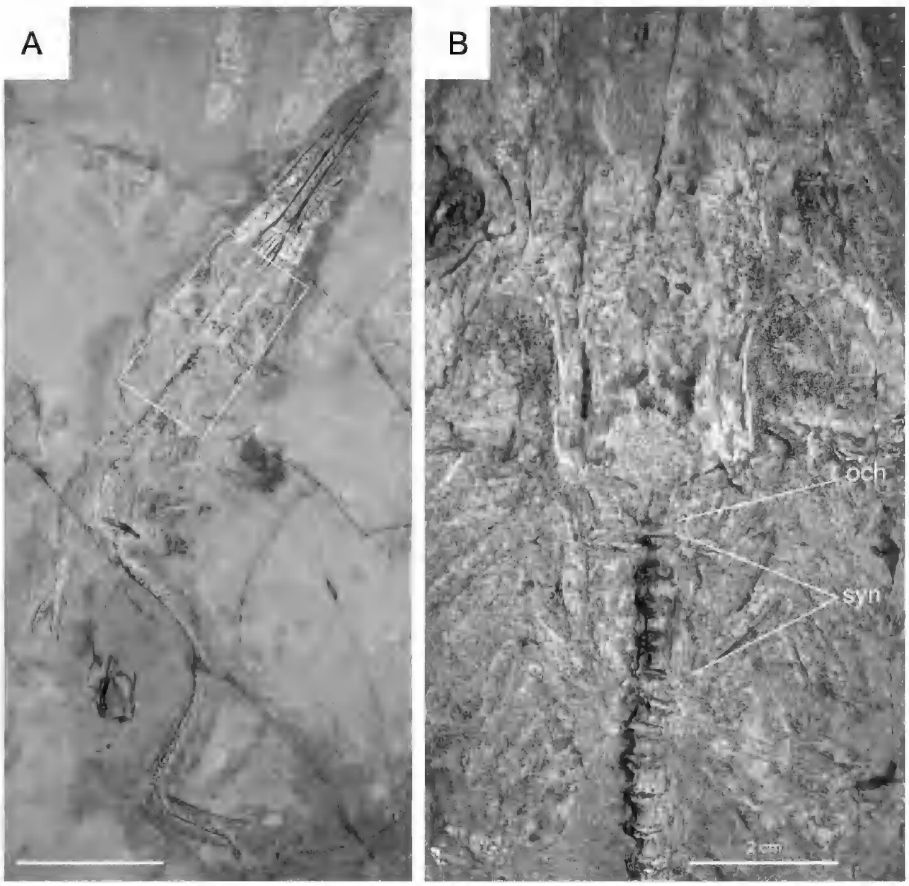

FIG. 14. An undescribed Early Jurassic batomorph skeleton from Holzmaden (SMNS 52666): **A,** general view of the specimen in dorsal view; white rectangle indicates region shown in B (scale bar = 10 cm); **B,** detail of cranio-vertebral articulation, showing the existence of an occipital hemicentrum and a short synarcual with four unreduced anterior vertebral centra. In all modern batoids, the occipital hemicentrum and the anterior-most centra within the synarcual are absent and the cranio-vertebral joint is formed entirely by fused dorsal and ventral arcualia of the vertebral column (synarcual cartilage). Thus, reduction or absence of the anterior spool in the first free centrum of squatiniforms is probably independent of the condition in batomorphs.

the synarcual centra extend farther anteriorly than in modern taxa (e.g., *Kimmerobatis*; Underwood and Claeson, 2017; *Spathobatis*; Claeson and Hilger, 2011). Claeson (2011) noted a trend within major extant batomorph clades, whereby the total number of vertebral centra flanked by the synarcual cartilage decreases among more derived taxa. The batomorph fossil record thus suggests that fusion of anterior basiventral and basidorsal cartilages to form a synarcual cartilage occurred only (1) after the evolutionary divergence of stem batomorphs and selachimorphs and (2) prior to the loss of the anteriormost vertebral centra and the occipital hemicentrum, whereas the hypnosqualean hypothesis implies the opposite (i.e., reduction and loss of the craniovertebral connection in squatinids and pristiophorids, prior to the fusion of anterior vertebral arcualia).

Most Late Cretaceous squatinid teeth from North America have been referred to *Squatina hassei* (Case and Schwimmer, 1988; Robb, 1989; Hartstein et al., 1999; Case et al., 2001; Becker et al., 2006). However, Guinot et al. (2012) considered that only one North American record (from the Late Maastrichtian of New Jersey; Case et al., 2001) relates to this nominal species. Bourdon et al. (2011) have suggested that many of the North American records of *Squatina hassei* represent an unnamed taxon with teeth resembling those of *Parasquatina*, which was tentatively included in the Squatinidae by Guinot et al. (2012). The latter authors also reformulated the genus *Cretascyllium* Müller and Diedrich, 1991, based upon features of the dentition (supposedly including high monognathic and moderate ontogenetic heterodonty) and placed both *S. hassei* and *C. cranei* within the genus *Cretascyllium*, which they regarded as a subgenus of *Squatina* (an opinion challenged by the findings presented here). Although such heterodonty has been reliably demonstrated in articulated specimens of *C. cranei*, its presence in *S. hassei* (which is still known only from isolated teeth) is inferential. Conversely (but again based on dental features), Cappetta (2012) has suggested synonymy between *Cretascyllium* and *Pseudorhina* rather than with *Squatina*, a view that is also challenged by the present findings. We also found no evidence to support a phylogenetic relationship between *Cretasquatina* and *Cretascyllium*; an articulated specimen of *C. cranei* shows the first centrum articulated with the occipital hemicentrum (BMNH P. 12213; Guinot et al., 2012: fig. 5), unlike in *Cretasquatina*.

It is possible that some of the Late Cretaceous teeth from North America previously assigned to *Squatina hassei* may pertain to *Cretasquatina* rather than to *Squatina* or *Parasquatina*. At present, *Cretasquatina* is known only from the Late Cretaceous of North America (Alabama and New Jersey). Future discoveries of holomorphic fossils associated with name-bearing teeth and exhibiting morphological features of *Cretasquatina* will hopefully clarify the systematic status, geographical distribution, and stratigraphic range of this taxon. Although *Cretascyllium* has been classified as a "subgenus" of *Squatina* (Guinot et al., 2012), it is resolved in the present phylogenetic analysis as a stem squatinid, closer to *Squatina* than either *Cretasquatina* or *Pseudorhina*.

Both localities from which *Cretasquatina* has been recovered are of Late Cretaceous (probably Campanian) age. The Mooreville Chalk at the Harrell Station site in Alabama was deposited in epicontinental marine conditions within the eastern edge of the Mississippi Embayment (a shallow, open-end, intracratonic basin; Pryor, 1960). The Ramanessin Brook locality of New Jersey is part of a transgressive-regressive marine sequence that formed on the eastern continental shelf of North America, with most of the vertebrate fossils coming from a Late Campanian lag deposit (Callahan et al., 2014). Paleogeographic reconstructions for North America during the Late Cretaceous indicate the presence of shallow seas connecting these two areas. *Cretasquatina americana* could therefore have had a geographical distribution extending from the Mississippi Embayment along much of the Atlantic littoral of North America, perhaps extending even farther westward into the Western Interior Seaway. Other marine fishes also occur in both regions, including elasmobranchs (e.g., *Scapanorynchus*, *Cretalamna*, *Squalicorax*), chimaeroids (*Ischyodus*), and teleosts (e.g., *Enchodus*, *Anomoeodus*, *Xiphactinus*), as well as sea turtles (e.g., *Peritresius*). Modern species of *Squatina*

are all confined to sea-shelf environments; some species are highly endemic (e.g., *S. formosa* in Taiwan), while others are more widely distributed (e.g., *S. dumeril* along the eastern seaboard of North America, across the Caribbean to the coast of Venezuela; *S. californica* along the entire western seaboard of North and South America), but none is pandemic or occurs on both sides of a major ocean (Compagno et al., 2005). The area connected by the two *Cretasquatina* occurrences documented here is thus comparable in size to the geographic range of some modern *Squatina* species.

Size comparison with skeletal elements of modern *Squatina* suggest that the individuals represented by the Harrell Station site were between >0.5 and >1 m in total length, which falls within the size range of modern *Squatina*.

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